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A SYSTEMATIC STUDY OF THE SALICACEÆ.

(*Concluded.*)

D. P. PENHALLOW.

ANATOMY.

The Growth Rings.— So far as may be judged from an examination of fifteen species of Salix and eleven species of Populus, growth rings of somewhat great radial extent appear to be a general characteristic of the Salicaceæ. Such a feature is directly correlated with, and in fact may be taken to be a resultant of the very free growth for which the members of this family are, in general, conspicuous. Partial exceptions have been observed in the medium growth rings of *Populus balsamifera*, *P. monilifera*, and *P. heterophylla*, as also of *Salix scouleriana*; but slight deviations of this nature cannot be regarded as expressing a general law, since as has been shown by Peirce (: 04), they may well have arisen in response to injuries inflicted by insects or other agencies, or they may simply be an expression of periodicity in climatic conditions. The same statement cannot be said to hold true in equal measure of *Populus alba* and *P. grandidentata*, since in both of these species the generally narrow and uniform growth rings seems to point to specific differences. These observations are greatly strengthened by the fact that *Salix uva-ursi* presents a noteworthy deviation from the general characteristics of the family. Its growth rings are not only narrow, but they are variable and strongly eccentric. Such characteristics are very readily understood when the natural habitat of this plant is recalled. Growing in the Alpine Garden on Mt. Washington at an elevation of about five thousand feet, its development is accomplished under the influence of a very short season the character of which must vary in an exceptional manner from year to year, while the prostrate habit would also establish marked eccentricity of growth. This case is therefore to be regarded as lying outside the normal course of development for the family as a whole, while at the same time it serves to give emphasis to the specific effects of external influences in modifying the character of the growth.

It is a general feature of the Salicaceæ to which there are no well defined exceptions of a noteworthy character, that there is substantially no differentiation of spring and summer wood. Partial exceptions seem to be shown by *Salix longifolia* in which the last six rows of cells sometimes become radially compressed, or by *S. cordata* and *S. lævigata* in which three rows are sometimes so modified. The fact that in all these cases the modification is not a constant feature, but that it arises sporadically, indicates clearly that it is due to some exceptional and transitory influence, and that it does not in any way express the usual characteristics of growth. On the contrary, it is not an uncommon feature in *S. nigra* for the first half of the growth ring to present the most dense structure, this being due, not to a diminution of the vessels with a relative preponderance of the fibrous mechanical cells, but to the fact that the latter are characterized by thicker walls than elsewhere, with a corresponding diminution of the cell cavity. In the investigated species of poplar, there seems to be no deviation from the general rule thus expressed. In both genera there is substantially no alteration in the form and size of the wood cells as between those of the inner and those of the outer face of the growth ring (Figs. 6, 7), and the demarcation between the growths of successive seasons is determined by other factors of which the occurrence of a limiting zone of resinous wood parenchyma is the most important. From these considerations it appears that the character of the growth ring, in its more general aspects, possesses no diagnostic value for specific purposes, or even for generic differentiations, but that it may be regarded as of value for ordinal purposes with respect to their great breadth and the absence of any marked differentiation between the spring and summer woods. Since the radial compression which is generally so distinctive a feature of the summer wood, is recognized to result from increasing cortical pressure (De Bary, '84, p. 501) it must be inferred from the observed structural conditions, that in the Salicaceæ as a whole, the bark expands or ruptures in such a way as to provide a minimum of pressure which is practically uniform during the entire period of growth.

The Transition Zone.—The protoxylem region in the Salicaceæ, or what may with more propriety be termed the *transition zone* in accordance with the previous use of that term (Penhallow, : 00, : 04c), is exclusively confined to the growth of the first year in accordance with the general law of growth which governs the Dicotyledonous angiosperms, and the following observations must therefore be interpreted in that sense.

So far as our studies have gone, they show that in the arborescent Salicaceæ, whether Populus or Salix, the transition zone is narrow and that it consists almost exclusively of a few spiral and scalariform elements. I have as yet been unable to discover in such forms, any extension of the protoxylem which would admit of transitional forms of the elements. The transition from the primitive protoxylem elements on the one hand, to completed forms of wood cells without pits, and of broad vessels with hexagonal pits on the other hand, appears to be developed with great abruptness. These features appear to be so well defined and constant as to make it apparent that the transition zone has been so far reduced as to approach the point of actual extinction.

In 1897 an opportunity was presented to collect some stems of *Salix uva-ursi* from the Alpine Garden, Mt. Washington. At that elevation the greatly reduced shrubs are forced to assume a prostrate habit of growth, in consequence of which the rather slender and somewhat sinuous stems are buried under a considerable accumulation of plant *débris*. In such situations, although there is usually an abundance of water during the summer, the plant is of a somewhat xerophilous habit as made evident by the reduced and somewhat coriaceous foliage, in obedience to the low temperature and the consequent inability of the roots to provide for an actively moving transpiration current, as pointed out by Schimper (: 03). This xerophilous habit is also expressed in the general structure of the wood as may be observed by reference to the diagnosis, from which it will be noted that the vessels are very small and there is a relative preponderance of the mechanical tissue. Assuming that the willows originated under the influence of a relatively warm climate as we have reason to believe must have been the case on the basis of evidence brought forward by Wieland (: 03), it is evident that *Salix uva-ursi* in common with other boreal and alpine forms, must represent a degenerate type which has been reduced under the influence of a diminishing temperature. But such reduction has clearly involved a loss of the originally erect position, and in consequence of the diminished necessity for mechanical support, it might be inferred that there would be a more or less pronounced tendency to reversion in such wise that the transition zone would tend to regain its primitive character to some extent, and that it would once more exhibit those developmental features of structure which have essentially disappeared from the great majority of species as now known. It was therefore felt that this plant might offer exceptional opportunities for a solution, in part at least, of the question as to the actual genesis of the vessels and the wood cells, and their mutual relations. The stem selected for study was of a somewhat sinuous form and in cross section ovate, the diameters being 1.20 and 1.80 cm., with the pith eccentrically placed toward the narrower or under side, the major axis of the cross section being oriented vertically. Longitudinal sections were cut from this stem at a slight angle with its principal axis, and in such number as to embrace not only the entire pith, but a considerable portion of the secondary xylem lying on opposite sides. It will thus be observed that while some of the sections were strictly radial, their character gradually changed as the relation of the plane of section to the radius changed, until they became strictly tangential. It thus became possible to study the elements of the transition zone from these two points of view and in a progressive series. But owing to the slight inclination of the plane of section to the longitudinal axis of the stem, the same section would exhibit at one end the radial aspect and at the other end the tangential aspect, while between the two there would be a graduated series of changes showing all details in the entire radial extent of the transition zone. This was found to be of special importance because the protoxylem is so localized and forms such small groups, while the transition elements are so scattered, that many radial sections might be examined without furnishing conclusive results. The diagonal plane of section, on the other hand, cuts through the entire radial extent of the transition zone and is certain to display whatever transition forms may be present. In this way it was possible to obtain the figures now presented.

The rather scanty pith is composed of isodiametric and somewhat thick-walled cells of large size, which, at the periphery, become greatly reduced in size without any diminution of the absolute thickness of the walls, assume the form of short cylinders, and function as resin-bearing parenchyma. There is thus produced a strongly resinous zone of tissue in immediate contact with the protoxylem and enclosing it on the radially inward face as well as the two tangential faces. It is not difficult to determine that the protoxylem consists primarily and chiefly of the usual spiral and scalariform tracheids which are common to the same zone in others of the Salicaceæ; but a careful examination of the diagonal section shows that there are other elements of a transitional character not to be met with, so far as I am aware, in other species having an upright habit of growth. A somewhat detailed account of the features noted will be essential.

The protoxylem elements proper consist of a few spiral tracheids characterized by very flat and close spirals. Such elements commonly have very abrupt and often transverse terminations. The length varies very much, so that while in most cases long, they are also not infrequently very short. As exposed in section on the tangential walls, the spirals are seen not to be simple bands, but to be broadest in the part which was most recently formed, and therefore most remote from the primary wall. The general effect of this is to give to the sectional view of the wall, the appearance of a continuous series of contiguous, bordered pits. This fact also makes it clear that the spirals of Salix have lost the simple and primitive character of those bands which are to be met with in the protoxylem of the gymnosperms, or even in many of the vessels of the Monocotyledons, and that they have distinctly approached that modification which must immediately precede the formation of bordered pits. Such a feature serves to show that the transition from spiral to scalariform structure might be accomplished without any very conspicuous transitional forms such as have been shown to exist in the case of Cordaites, and such as are found not to exist in the Salicaceæ as a rule; while it also serves to explain in part the great radial diminution of the protoxylem of the Salicaceæ as compared with that of more primitive forms of plants. In addition to the spiral tracheids, the protoxylem also includes a certain number — generally few — of scalariform elements. These approximate in form and size to the spiral tracheids though they often have distinctly tapering extremities, in which respect they approximate very closely to the fibrous mechanical elements or wood cells of the secondary xylem (Fig. 1). It has also been observed in such cases, that the scalariform markings become distinctly fewer and more distant (Fig. 1) as if certain of the pits had been obliterated by a more general secondary thickening of the wall, and that such is the true explanation we are justified in believing from a study of the transition zone in Cordaites (Penhallow, :00, :04c). That such obliteration has not proceeded at a uniform rate throughout the length of the cell, is evident from the figure given. When such scalariform markings are exposed in section, they exhibit precisely the same bordered structure as in the case of the spirals. The most interior portion of the secondary xylem sometimes contains scalariform elements of a transitional form. In such cases the scalariform structure is irregular and very imperfectly developed upon both the radial and the tangential walls, presenting an obvious form of transition in the direction of the bordered pits, chiefly expressed in the shortening of the individual pits and their more definite segregation. But such changes in the structure of the cell wall might equally well be precedent to the complete and final obliteration of the pits of whatever form,

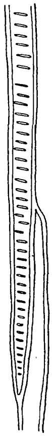

FIG. 1.— *Salix uva-ursi.* Tangential section of a scalariform tracheid showing transitional form. × 350.

a view which is justified not only by the reduction in size and number of the scalariform markings, but by the irregular manner in which such reduction proceeds, so that the pits often lack that regular and definite disposition so characteristic of the bordered pits; and finally it is justified by the fact as shown in Fig. 1, that the scalariform markings are often wanting on the radial walls while characteristically developed on the tangential walls.

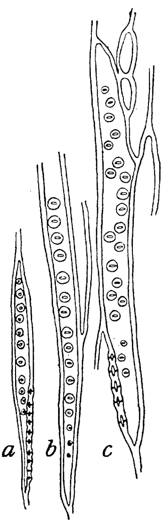

Fig. 2.—*Salix uva-ursi.* Tangential sections of tracheids with bordered pits, showing transitional forms in the direction of fibrous wood cells. × 350.

The earliest secondary xylem is characterized by the presence of true fibrous tracheids distinguished by the presence of bordered pits. These tracheids as shown in Figs. 2 and 3, are all tapering or of the fibrous and fusiform type, and they vary very much in length and breadth. In those of the most slender form, there is but a single row of bordered pits which diminish very greatly in size as the end of the tracheid is approached (Figs. 2, *a*, *b*). With an increase in breadth and usually a corresponding diminution of length (Fig. 2, *c*), there is a strong tendency to a multiseriate arrangement which becomes fully expressed in the completely developed vessel as shown in Fig. 5. In such fibrous tracheids, there is considerable variation in the distribution of the bordered pits. Thus we find many instances of pits on both the radial and tangential walls (Fig. 3), a distribution common to the vessels as shown in Fig. 5, although it will be noted that when such a vessel abuts upon a fibrous wood cell, there are no bordered pits on the radial wall common to the two. This fact is expressed in other ways. Thus in the case of the fibrous tracheids in Fig. 2,

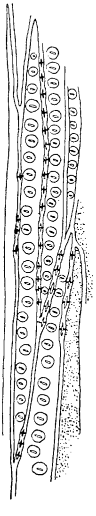

Fig. 3.—*Salix uva-ursi.* Tangential section showing transitional forms of tracheids with bordered pits on both the radial and the tangential walls, and resinous wood cells. × 350.

it will be seen that the pits are confined chiefly to the tangential walls, and appear on the radial walls at the ends only of the tracheids (Figs. 2, *a*, *c*), or they may even be completely eliminated from the radial walls as in Fig. 2, *b*. Such variations are also to be seen in Fig. 4. One variation of such relations worthy of note, was found in radial section. A spiral tracheid of the protoxylem was immediately followed on its outer side, by a fibrous tracheid with round, variably distant bordered pits in one series. The tangential wall common to the two was also provided with a continuous series of bordered pits. Immediately outside the fibrous tracheid, and therefore on the side opposite the spiral tracheid, was a fibrous wood cell presenting no pits of any kind upon either its radial or its tangential walls. The illustrations thus given in detail, serve to illustrate the general fact that all sorts of transitional forms are to be found, connecting the fibrous elements of the secondary xylem with the cylindrical and more or less tubular elements of the protoxylem; and it is quite evident that we have in *Salix uva-ursi* the same sort of a transition zone as that which has already been shown to exist in the gymnosperms (Penhallow, :00), the two cases differing chiefly with respect to (1) the radial extent of the zone, (2) the number and extent of the transition forms, and (3) the specific character of the final products. When we consider the various transformation stages occurring in *Salix uva-ursi*, the peculiar conditions of reduction in the structural details of the cell wall, the special alterations in the form of the individual elements, and the peculiar association of these derived forms, it is exceedingly

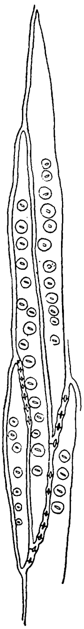

FIG. 4. — *Salix uva-ursi.* Tangential section showing various phases in the evolution of the fibrous wood cell through the pitted tracheid. × 350.

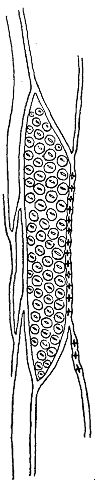

FIG. 5. — *Salix uva-ursi.* Tangential section of a vessel showing its relation to fibrous wood cells, the multiseriate bordered pits on both radial and tangential walls, and its deviation from the type of the fibrous tracheid. × 350.

difficult not to feel that we have before us an expression of evolution in two directions from the protoxylem, the one leading directly to the formation of vessels with multiseriate bordered pits; the other leading to the formation of purely mechanical and fibrous elements wholly devoid of pits, or in which the latter survive in the form of simple, sporadic perforations of small size. As far as it is possible to interpret the alterations of structure so far observed, the following would seem to be the sequence of events : —

Protoxylem.

Spiral tracheids with close spirals set at a low angle and showing a bordered pit structure in section. Terminations usually abrupt.

Scalariform tracheids with abrupt or tapering extremities; the markings showing a bordered pit structure in section. Transitional forms numerous. Markings often obliterated from either the radial or the tangential walls.

Secondary Xylem.

The elements diminish in length and increase in breadth.

The bordered pits on both the radial and the tangential walls are successively 1-, 2-, and multiseriate.

The vessels thus formed are multiplied in large numbers ; they serve the purpose of circulation ; they are reproduced as features of the secondary wood of each year's growth ; they do not form a definite zone or medullary sheath after the first year; their functional activity may be arrested by the excessive development of thyloses or other causes; they constitute a relatively small portion of the entire structure; they contribute to the greater porosity and diminished strength of the structure as a whole.

The elements diminish in breadth and increase in length.

Bordered pits are at first present on both the radial and the tangential walls; at first one-seriate, they diminish in number and become more strictly segregated ; they become more strictly confined to the radial walls ; they eventually disappear ; the secondary wall becomes of uniform thickness throughout, rarely with simple and minute pits. The mechanical elements or wood cells thus formed, are concerned solely with meeting the requirements of stress, to which end they are especially adapted ; they constitute the chief part of the secondary xylem as of the secondary growth of the stem, to which they impart hardness, solidity, rigidity, and durability.

A comparison of these evolutionary phases with those already determined for Cordaites (Penhallow, :00, p. 57, and :04c, p. 250) will show that the two are essentially parallel, differing from one another only in detail in the two directions already indicated. So far then as the Salicaceæ are concerned, there is abundant supplementary evidence to show that in that family as well as in the gymnosperms, the evolution of the secondary xylem from the protoxylem is determined by the special requirements of support and the movement of the transpiration current; that the fibrous, non-pitted wood cells serving the ends of mechanical support, are derived from the spiral tracheids in the first instance; and that the relative predominance of mechanical or conductive tissue, is the *resultant* of influences acting along two distinct lines of development.

The Wood Cells.—Very little diagnostic value attaches to the appearance or disposition of the wood cells as presented in transverse section, and such features as they do exhibit are rather of ordinal than of generic or specific value. They are always hexagonal and very variable as to size. Usually they are disposed in a very irregular manner, though occasionally there is a more or less pronounced tendency to disposition in radial rows, but in no case is this so pronounced as in the Coniferæ — a difference which may be said to distinguish the gymnosperms from all the higher types of woody plants. The walls are of medium thickness, a feature which seems to be consistent with the generally soft character of the woody structure, and, as already pointed out, there is a complete absence of that unequal, regional, secondary growth of the cell wall which, in other woods, contributes so largely to a differentiation of the spring and summer woods. On the whole, the structure of the mechanical tissue is closely comparable with that of the Rhamnaceæ, a resemblance which will be found to extend to other features of the vascular zone.

Wood Parenchyma.— In its transverse section, the wood parenchyma varies considerably according to its position in the structure. Within the region of the medullary sheath the elements are more or less isodiametric; when associated with vessels, the tendency is to compression conformably with the radius of the vessel; when forming isolated tracts, they tend to assume the form of the associated wood cells; but when occurring in the limiting zone of a growth ring where they are chiefly to be met with, they are invariably compressed in a radial direction, thereby assuming a form which serves to distinguish them from the associated mechanical elements.

In their longitudinal aspects there is little that is not common to such elements wherever they may be found. They are cylindrical elements with somewhat thick and pitted walls, and abrupt or transverse terminations. In the medullary sheath they are generally only a few times longer than broad, but within the region of the secondary xylem, and especially in the limiting zone of the growth ring, they become much longer and proportionately narrower. Such features, however, whether exhibited in transverse or longitudinal section, are of an altogether gen-

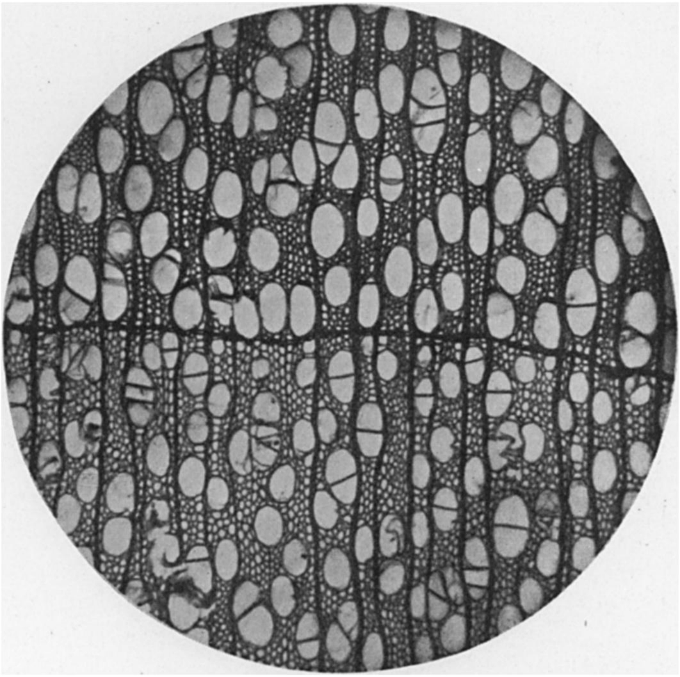

FIG. 6.—*Salix alba*. Transverse section showing characteristic structure of the genus. × 52.

eralized type, and they possess no value for differential purposes. The wood parenchyma is always characterized by the presence of resinous matter which is generally deposited in large quantity, and it thereby gives a distinguishing feature to the elements which admits of their very ready recognition. This is especially true of them in the region of the medullary sheath, but it is also equally true in some other cases.

The distribution of the resinous wood parenchyma as displayed in transverse section, presents features of special value for diagnostic purposes. In all of the Salicaceæ it forms a thin, limiting zone on the outer face of the growth ring. This zone varies somewhat in thickness and continuity, but as a rule it is composed of a continuous series of cells forming a layer from one to three elements thick (Figs. 6, 7). But in the

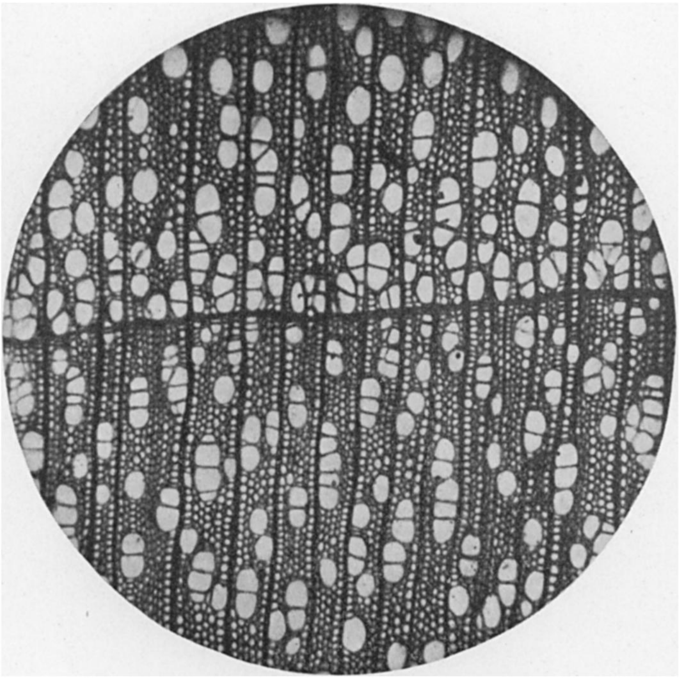

FIG. 7.—*Populus tremuloides.* Transverse section showing the characteristic structural features of the genus. × 52.

genus Salix, other features of importance for differential purposes are presented. Thus in *S. cordata* the cells occur in large numbers throughout the woody zone, and are distributed in such manner as to form rather conspicuous and often somewhat extensive tracts disposed without any reference to an orderly arrangement. In *S. sessilifolia* and *S. longifolia*, it not only occurs in the limiting zone, but it is also definitely associated with the vessels as in *S. cordata*, forming about them a narrow but discontinuous layer, or as isolated cells at various parts of the periphery. All other species of Salix, so far as indicated by present investigations, have the wood parenchyma confined to the limiting zone of the growth ring, a rule which also seems to apply to Populus without exception.

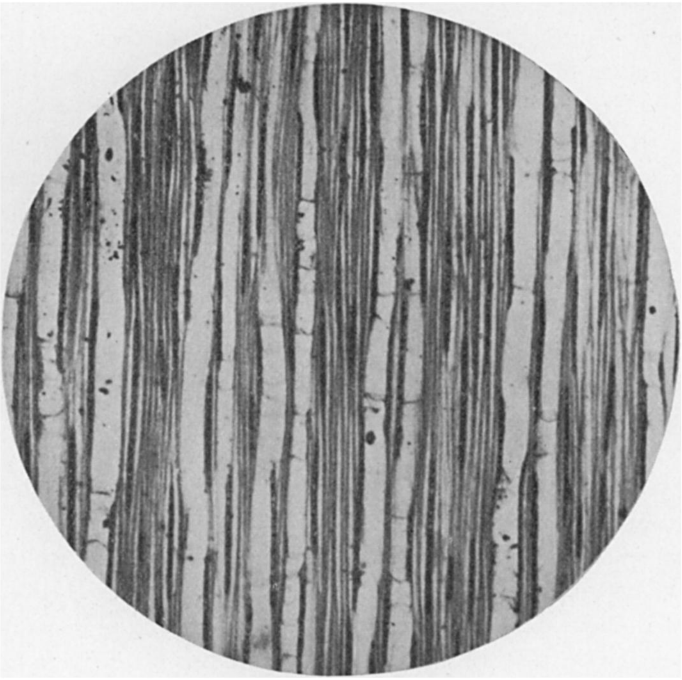

FIG. 8.—*Populus tremuloides.* Tangential section. × 52.

The Vessels.—The chief diagnostic value of the vessels is to be found in their distribution and compounding as exposed in transverse section, but before considering these features, it may be well to discuss the few details relating to their aspects in longitudinal section.

Thyloses are a general feature of the vessels in wood of the Salicaceæ, but they differ in some important essentials from those with which we are familiar in other woods, *e.g.*, Catalpa or Pinus. They generally fill the cavity of the vessel so completely (Figs. 6, 7) that in transverse section they seem to be entirely wanting. This is due to the fact that they undergo no longitudinal division, and as a result there is only one thylosis transversely, which is closely applied to the wall of the vessel. It will nevertheless be observed that in longitudinal section, instead of the modified spherical form usually assumed in woody stems, the thyloses of the Salicaceæ are really in the form of long, cylindrical cells several times longer than broad, but of very variable length. It is this last feature among others, which results in their apparent absence from the transverse section, since a given plane of section is most likely to pass between terminal walls, and as the thyloses lie in a single series, there are no longitudinal walls to break up the cavity of the vessel.

Apart from the well known structure which distinguishes all the vessels of the wood in angiosperms, it will be found that the radial walls are characterized by bordered pits which are chiefly somewhat distant, sometimes conspicuously so, and in consequence they are either oval or round (Fig. 10). It is rather the exception that they are so aggregated as to become hexagonal. On the other hand, in the tangential section, the pits are invariably crowded together to such an extent that they are typically hexagonal (Fig. 11), and the space between contiguous pits is represented by only a very narrow line of secondary wall joined directly to the primary wall. These differences will be found in exact accord with the distribution of the pits on the radial and tangential walls as described for the transition zone, and they seem to imply that the transverse movement of the transpiration current must be somewhat more energetic in a tangential than in a radial direction, contrary to what has been found to be the case in the Coniferales.

In transverse section the distribution, form, and compounding of the vessels impart to the structure an appearance quite similar to that found in the Rhamnaceæ. This very striking resemblance is likely to result in confusion unless very careful attention is given to details; and the likelihood of error from this source is all the more probable when it is observed that there is also a strong similarity of structural detail in radial section. It is, however, not our purpose to discuss these resemblances at the present moment, since the essential differentiations of the two families will be sufficiently emphasized by their separate study. In the Salicaceæ the vessels give to the entire structure a high degree of porosity which is extended more or less uniformly to the entire thickness of the growth ring (Figs. 6, 7). This general law is subject to variation in detail. Thus

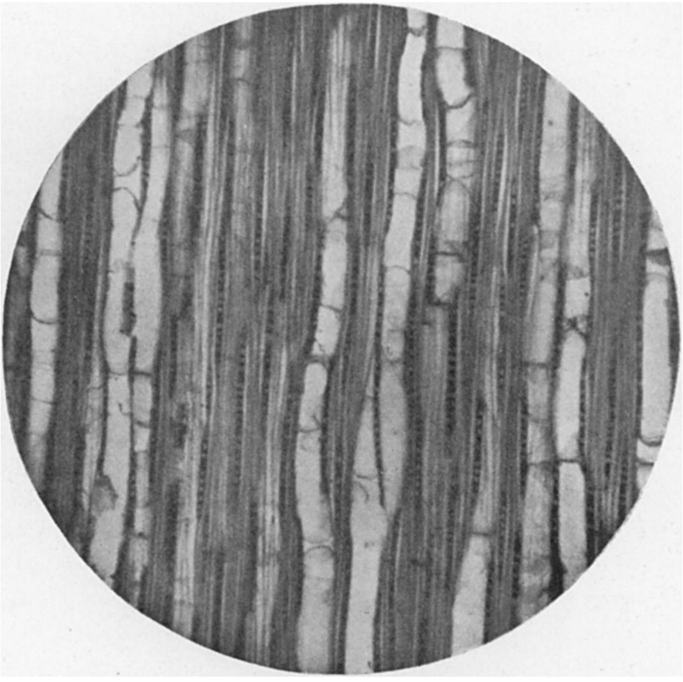

FIG. 9.—*Salix alba.* Tangential section. × 52.

in such types as *Salix alba* (Fig. 6), *S. lævigata*, or *S. longifolia* they are so abundant as to give the impression of predominance, an impression which is greatly strengthened in *S. lasiandra* where the vessels justify the description of "strongly predominant throughout." The same law of distribution also applies to the poplars, though with the very essential difference that while in Salix there appears to be no very essential numerical reduction as between the initial zone and that which terminates the growth ring (Fig. 6), in Populus on the contrary, the initial zone usually shows a great increase in numbers with a more or less gradual diminution toward the termination of growth for the season (Fig. 7). This is fully expressed in such species as *P. alba*, *P. wislizeni*, *P. angustifolia*, etc., but in *P. monilifera* there seems to be a predominance which is fully maintained until the region of the summer wood, when there is an abrupt reduction.

The form of the vessel is typically oval in a radial direction (Fig. 7), but this is sometimes varied to oblong as in *Salix alba* (Fig. 6) or *S. lævigata*, or to broadly oval as in *Populus heterophylla*, or even to transversely oval as in *P. alba*. While in general, the vessels are largest in the initial growth of the season, the diminution in size toward the outer face of the growth ring may proceed gradually and without any very marked alteration as in *P. tremuloides* (Fig. 7); they may become abruptly smaller as in *P. fremonti*, or they may exhibit a graduated diminution as in *S. uva-ursi*.

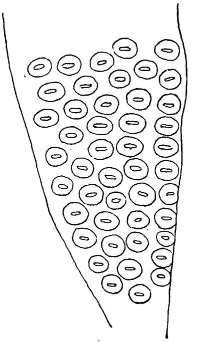

FIG. 10.—*Populus tremuloides*. Radial section showing the round or oval and distant bordered pits. × 350.

One of the most striking features of the vessels in the transverse section, is their peculiar compounding, a feature also similarly expressed in the Rhamnaceæ. Such compounding in the Salicaceæ always occurs in such manner as to give rise to radial series (Figs. 6, 7) and in the various forms of complexity thus arising, it constitutes within certain limits, a valuable differential character for the various species. Thus in *Salix longifolia*, *S. discolor*, *S. uva-ursi*, *Populus* *alba*, *P. fremonti*, *P. pyramidalis*, *P. balsamifera*, etc., the large, oval vessels later become reduced in size, but they chiefly remain single or become sparingly 2-compounded. In *Salix alba* (Fig. 6), *S. sessilifolia*, or *S. brachystachys*, the vessels are chiefly 1-, 2-, or rarely 3-compounded; in *S. nigra*, they are rarely 8-compounded; in *S. lasiolepis* they are chiefly single throughout; in *S. lancifolia* they are rarely 4-compounded; in *Populus fremonti* they are rarely 5-compounded, and similar variations are to be met with throughout the entire family, always with the status of specific characters. While the general facts are thus noted, it will be sufficient to refer to the various diagnoses for an amplification of such details. It is only occasionally that the vessels assume a definitely resinous character. This is expressed among the species so far investigated, only by the unusually resinous *Salix cordata*, the vessels of which are everywhere resinous.

Medullary Rays.—As in the Coniferales so in the Salicaceæ, the medullary ray presents some of the most important of all the structural features for diagnostic purposes. Their value is of both a generic and a specific character. They are expressed in both radial and tangential sections which it will be desirable to discuss separately somewhat in detail.

In their tangential aspects the medullary rays of the Salicaceæ may be described as chiefly narrow; 1- or more rarely 2-seriate in part. From this there is no essential deviation which applies to one genus more than to the other, except in so far as variation is rather more characteristic of Salix, and constancy more characteristic of Populus. It may be said that broad rays, or rays with oval or transversely oval cells, and 2-seriate rays are more common to the former than to the latter. Such differences will be made sufficiently clear by a comparison of Figs. 12 and 14, and Figs. 12 and 15.

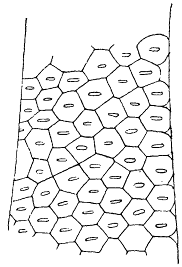

FIG. 11.—*Populus tremuloides.* Tangential section showing the multiseriate and hexagonal bordered pits. × 350.

One of the chief factors in the tangential section of the ray, is the occurrence of ray cells of two kinds and the possibility of distinguishing them from one another. These cells will be referred to as (1) and (2), and their more detailed characteristics will be discussed in connection with the radial section. In the genus Populus, as clearly shown in *P. tremuloides* (Figs. 12, 13), there is no clearly defined distinction between the two kinds of cells by means of which each may be recognized beyond question. In Fig. 13, the distinction is clear by reason of the distribution of the resin and the special location of each kind of cell. Thus the more resinous cells, *a*, occupying the central region, are of the first order (1), while the less resinous cells, *b*, occupying the extremities of the ray, are of the second order (2). This differentiation serves to illustrate the general law that the cells of the first order are usually the more strongly resinous, and that the less resinous cells of the second order are chiefly terminal unless also interspersed. But such distinctions are not always valid, even in the same species, since in Fig. 12, taken from the same section, the non-resinous terminal and interspersed cells, *b*, are probably all of the second order, while the more resinous cells, *a*, are chiefly of the first order. But the three resinous and terminal cells of this figure involve considerable doubt as to their precise character, inasmuch as their positions would lead us to assume that they must be of the second order in spite of their resinous contents, a view which gains force from what may sometimes be observed in radial section.

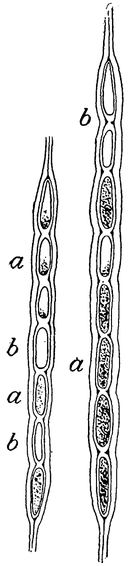

FIG. 12. — *Populus tremuloides*. Tangential section of the narrow medullary rays. *a*, cells of the first order; *b*, usually non-resinous cells of the second order. × 350.

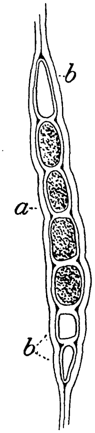

FIG. 13. — *Populus tremuloides*.—Tangential section of a medullary ray with broader and resinous cells of the first order, *a*, clearly distinguishable from the non-resinous and somewhat narrower cells, *b*, of the second order. × 350.

In the genus Salix (Figs. 14 and 15), where the structure is of a more decidedly resinous character, the cells of the medullary rays are usually all resinous, and this feature serves no useful purpose in differentiations. We do find, nevertheless, that in position and form, as also usually in size, there are differential features of well defined value. Thus in *Salix longifolia* (Fig. 14) there is no room for hesitation between the round or transversely oval cells, *a*, of the first order constituting the bulk of the structure, and the oblong narrow and terminal cells, *b*, of the second order. Or again in the same species (Fig. 15), the same difference appears in the 2-seriate form of the ray. In low rays, the tendency is for the cells of the first order to be replaced by those of the second order as also shown in Fig. 15 on the right. From these considerations it will be obvious that the distinctness with which these two forms of cells appear in the tangential section is of importance as a basis of generic differentiation.

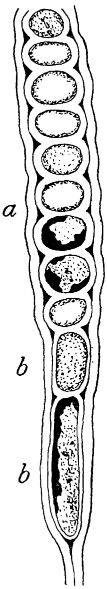

FIG. 14.—*Salix longifolia.* Tangential section of a medullary ray showing the resinous character of the cells; the round or chiefly transversely oval form of the cells of the first order, *a*, and the larger and narrower cells, *b*, of the second order, the two forms of cells being sharply differentiated. × 350.

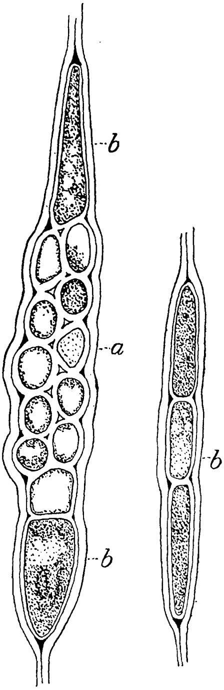

FIG. 15. — *Salix longifolia.* Tangential section of two rays, the one showing the 2-seriate form embracing cells of the first order, *a*, together with larger terminal cells, *b*, of the second order, the two clearly differentiated; the other showing a low ray entirely composed of cells, *b*, of the second order. × 350.

A second factor of value is to be found in the form of the ray cell and its variations. In the genus Populus, the cells of two kinds present little or no difference in form by which they may be distinguished from one another. This is especially true of *P. balsamifera*, *P. heterophylla*, *P. monilifera*, etc., while in *P. tremuloides* (Fig. 13), *P. alba*, *P. pyramidalis*, *P. grandidentata*, etc., there is a somewhat obvious difference in many cases which, taken in conjunction with other features, serves to bring such species into a separate group. Thus it will be found that where such differences exist, the cells of the second order are generally narrower and relatively or absolutely longer. The cells of the first order are, as a rule, chiefly narrow and oblong. Few exceptions to this occur (Fig. 15) though they may appear not only in the same species but also in the same section. On the whole it may be said that Populus is generally characterized by narrow and oblong cells — the tendency to an oval or round form being of the nature of an exception. In the genus Salix, on the contrary, the typical form of the cell (1) is oval, round or even transversely oval (Figs. 14, 15), the occurrence of narrow and oblong cells being of the nature of an exception. The cells of the second order (2) are also much longer and narrower than in Populus, differences which will be readily explained by the radial sections, so that considering these differences as a whole, they again afford a valuable element in generic differentiations.

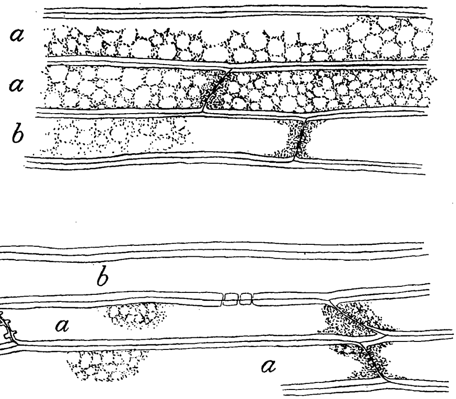

FIG. 16.—*Populus tremuloides.* Radial section of medullary rays showing the often resinous character and structural details in cells of the first order, *a*, and the second order, *b*. × 350.

The radial aspect of the medullary ray is, in many respects, the most important for diagnostic purposes inasmuch as it exhibits very striking differences of structure and form which are not only of generic but of specific value. These differences are expressed most prominently in the form and character of the cells whereby it is necessary to recognize cells of two kinds. Fundamentally the ray is composed of cylindrical cells several times longer than broad, and either of uniform width throughout or somewhat contracted at the ends. The terminal walls are always more or less strongly pitted, but they exhibit somewhat striking variations in this respect as between Salix (Fig. 17, *a*) and Populus (Fig. 16, *a*). The upper and lower walls are rather thick and often strongly pitted, but in both of these respects there is a marked difference between the two genera in such a way that in Populus (Fig. 16, *a*) there is always a tendency to a relatively thin wall with few pits, while in Salix (Fig. 17, *a*) the tendency is always toward a very thick and strongly pitted wall. Such cells are generally resinous, more strongly so in Salix than in Populus, and it is in them that resin is found when it may have been eliminated from all other parts of the ray. Such cells I have designated as "cells of the first order" or (1). They seem to be the more primitive parts of the structure, and in this sense they are comparable with the parenchyma cells of the gymnosperms (Penhallow, :04c). Their radial walls are generally devoid of pits except that in a few instances I have observed the occurrence of minute and simple pits opposite wood cells, but so far as can be ascertained at the present time, this feature possesses no special significance.

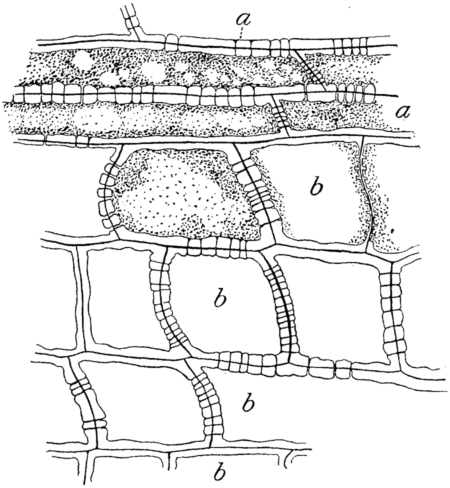

Fig. 17.—*Salix hookeriana.* Radial section of a medullary ray showing details in the structure of the cell walls: cells *a* of the first order, and cells *b* of the second order, the latter occupying a marginal position. × 350.

Together with the cells of the first order, cells of a somewhat and often wholly different character appear. In the genus Populus, this differentiation is expressed with the least force, and it is difficult or even impossible to distinguish between the two except through certain special structural features of the radial walls. Such cells are, generally speaking the least resinous. To all such I have applied the designation "cells of the second order" or (2). An inspection of Fig. 16 taken from *Populus tremuloides*, will show that there is essentially no distinction as to form and structure, between cells of the first order, *a*, and those of the second order, *b*, and it is only when we study such cells opposite vessels that the distinction becomes obvious. In such regions cells (2) invariably show either oval (Fig. 18) or quadrangular pits (Fig. 19) disposed in somewhat definite radial series. Such pits and of the forms described, are characteristic of the genus Populus, and from this there is no essential deviation so far as our investigations have proceeded. These features make it clear why the tangential section of a ray in Populus does not give a clear differentiation of the two kinds of cells. In the genus Salix the case is very different. There we always find the ray characterized by the presence of cells which are very much shorter and very much higher, so that they become isodiametric (Fig. 17, *b*). But it also very often happens that the alteration thus indicated is subject to extreme exaggeration in such a way that the cells become several times higher than long, and therefore *high and narrow*. This is a feature peculiar to Salix, and it has not been observed in any form in Populus. It is this very strong difference in form, as well as the very striking variations in size among the cells of the second order, which serves to establish so strong a differentiation between the two kinds of cells as exposed in tan-

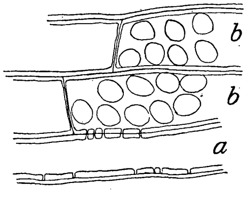

FIG. 18. — *Populus tremuloides*. Radial section of cells of the second order (2) showing oval pits on the lateral walls opposite vessels. × 350.

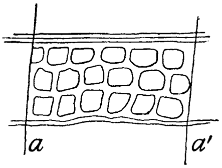

FIG. 19. — *Populus tremuloides*. Radial section of cells of the second order, (2) showing quadrangular pits on the lateral walls opposite vessels. × 350.

gential section. In addition, however, the cells (2) are always characterized by their peculiar pits on the radial walls when opposite vessels. These pits are very rarely of the oval or quadrangular form presented by Populus. On the other hand they are more or less definitely angled and crowded as typically presented by *Salix alba* (Fig. 20.) But such a form is subject to very marked and significant variation. Thus in such types as *S. sessilifolia*, the individual pits vary very greatly in size and form, sometimes being greatly reduced in size and multiplied in number, or again they diminish in number and increase greatly in size (Fig. 21); and not infrequently — indeed we might say that very often, even in the same species — there are all degrees of transition exhibited from the angled pit of *Salix alba* (Fig. 20) to typical scalariform structure in *S. sessilifolia* (Fig. 22). Such transitional forms are peculiar to Salix.

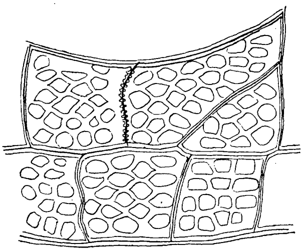

FIG. 20 — *Salix alba.* Radial section of cells of the second order (2), showing their form and the character of the angled pits on the lateral walls opposite vessels. × 350.

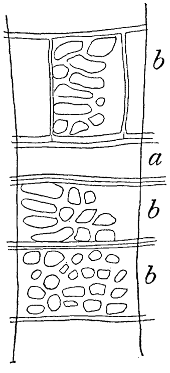

FIG. 21. — *Salix sessilifolia.* Radial section showing a cell, *a*, of the first order (1), and cells, *b*, of the second order (2) with variable, angled pits on the lateral walls opposite vessels, merging into scalariform structure. × 350.

In the genus Populus the distribution of the two kinds of cells is effected in such a way that those of the first order occupy the central region, while those of the second order occupy the margins above and below (Fig. 16, *b*, *b*; Fig. 13, *b*, *b*). Occasionally there is an interspersal with the cells of the first order (Fig. 12, *b*, *b*), but in such cases, as already pointed out, it is not always easy to distinguish the two kinds of cells, especially in a tangential section. In the genus Salix the same relation exists (Fig. 21, *a*), with the difference that interspersal is a much more common feature, and the distinction of the two kinds of cells may be made without any difficulty in any plane of section. The relations thus indicated show that there is a tendency toward replacement of the more primitive cells (1) by those (2) of a more advanced and specialized functional value; and this tendency is carried to such an extent that in low rays the replacement is often complete (Fig. 15). It is of interest from a developmental point of view to note that this relation is precisely that which has already been shown to exist among the higher gymnosperms, with respect to the relative preponderance of parenchyma cells and ray tracheids, and such a comparison goes far to prove, especially in connection with other relations to be described immediately, that the cells of the second order are of the higher type of development.

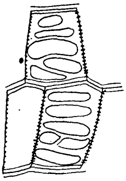

FIG. 22.— *Salix sessilifolia.* Radial section of a cell of the second order (2) showing complete transformation into scalariform structure opposite a vessel. × 350.

The features thus described for the radial section of the medullary ray, are of both generic and specific value as will be seen from the diagnoses given, but it should be pointed out that the recognition of two forms of cells in the medullary ray of the Salicaceæ is exactly parallel with what has already been noted as characteristic of the Coniferales (Penhallow, :04c), though with one important difference. In the gymnosperms the ray contains in its more primitive condition, parenchyma cells only, although these later become differentiated into two specialized forms. As a whole, these are equivalent, from the standpoint of development and functional value, to cells of the first order in the Salicaceæ. But in all the higher Coniferales the ray also contains specialized ray tracheids which manifestly provide greater freedom in radial circulation, and as already shown elsewhere, (Penhallow, :04c), such development is in direct response to the requirements of a higher type of organization. No such tracheids occur in the rays of the Salicaceæ, but they are exactly represented in a functional sense by the cells of the second order (2), which also serve as evidence of a higher type of organization.

While it is not our present intention to discuss the phylogeny of the Salicaceæ in detail, and to establish its relative position in the scale of evolution, it is desirable to indicate that the general trend of the evidence so far collected — geographical, geological, anatomical—is all in one direction, and that is to show that the genus Populus is essentially the more primitive member of the family, and that it is the genus through which we must probably seek connection with ancestral forms.

It only remains to point out that with respect to a delimitation of species and varieties, the rule adopted for the gymnosperms (Penhallow, :04c) applies with equal force here, to the effect that varieties have no proper status on anatomical grounds, and what are designated as such on the basis of external morphology must be regarded as species from the standpoint of the present studies.

SALICACEÆ.

Transverse.— Growth rings usually devoid of recognizable differentiation of spring and summer wood, the outer limits being defined by a usually resinous wood parenchyma of radially narrower cells, forming a zone upwards of three elements thick. Wood cells variable, hexagonal, and usually not in obvious radial rows. Vessels numerous throughout, often predominant, and more or less radially compounded.

Radial.— Medullary rays composed of two kinds of cells, *i. e.*, those without (1) and those with (2) pits on the lateral walls opposite vessels. Vessels commonly with thyloses, their radial walls with numerous, multiseriate, usually localized, oval, round, or hexagonal bordered pits.

Tangential.— Medullary rays chiefly narrow; 1- or more rarely 2-seriate in part. Vessels with numerous, multiseriate, hexagonal, bordered pits throughout.

1. **Populus.**

Radial.— Ray cells of two kinds but presenting no essential distinction as to length, height, and thickness of the walls: the pits on the lateral walls of cells (2) more definitely rounded, oval or sparingly angled, when they become quadrangular and lie in radial series, never merging into scalariform structure.

Tangential.— The two kinds of ray cells not clearly distinguishable.

SYNOPSIS OF SPECIES.

Ray cells (2) (tangential) more or less distinguishable by differences in height, breadth, and less resinous contents.

Rays (tangential) 2-seriate in part.

Ray cells (1) somewhat variable, oblong, narrow, or broader and oval; unequal.

Vessels (transverse) broad, oval, 1- to 3-, more rarely 5-compounded. 1. *P. fremonti.*

Rays (tangential) strictly 1-seriate.

Ray cells (1) (tangential) uniform, narrow, oblong, equal, but occasional rays with broader, oval, and somewhat variable, unequal cells.

Vessels (transverse) broad, oval, or transversely oval, 1- to 2- or rarely 4-compounded. . . . . . . 3. *P. alba.*

Vessels (transverse) broadly oval, 1- to 4- or rarely 7-compounded. 4. *P. tremuloides.*

Ray cells (1) (tangential) uniform, narrowly oblong, and equal, but in different rays sometimes broadly oblong.

Vessels (transverse) very numerous, broad, 1- to 3- or rarely 4-compounded. . . . . 5. *P. pyramidalis.*

Vessels (transverse) numerous, much smaller toward the outer face of the growth ring, 1- to 4- or rarely 5-compounded. 6. *P. grandidentata.*

Ray cells (2) (tangential) not distinguishable from (1).

Rays (tangential) all strictly 1-seriate.

Rays (tangential) with diminishing terminal width.

Vessels (transverse) at first predominant, gradually diminishing in size and number, 1- to 3-, rarely 4- to 5-compounded. 7. *P. wislizeni.*

Rays (tangential) of uniform width throughout.

Vessels (transverse) numerous, oval, 1- to 4- or rarely 5-compounded. . . . . 8. *P. balsamifera.*

Vessels (transverse) at first predominant, gradually diminishing in size and number; 1- to 4-, rarely 6-compounded. 9. *P. angustifolia.*

Vessels (transverse) numerous throughout, abruptly smaller in the outer portions of the growth ring; 1- to 4-compounded. 10. *P. trichocarpa.*

Vessels (transverse) numerous, large, oval, or round, often in series continuous and compounded with those of the previous season; chiefly single but often 2-, and on the outer face of the growth ring sometimes 3-compounded. . . 11. *P. heterophylla.*

Rays (tangential) 2-seriate in part.

Rays (tangential) uniform in width throughout.

Vessels numerous throughout, broadly oval, abruptly fewer in the region of the summer wood, chiefly single, or less frequently 2- to 3-compounded. . . . . . 2. *P. monilifera.*

1. *P. fremonti* Wats.

Transverse.— Growth rings very broad, the limiting zone of wood parenchyma devoid of resin, 1 to 2 cells thick. Vessels large, broad, oval, becoming somewhat abruptly smaller toward the outer limits of the growth ring; 1- to 3-, more rarely 5-compounded. Rays numerous, sparingly resinous, one cell wide, distant upwards of 12 rows of wood cells.

Radial.— Ray cells (1), the upper and lower walls thin and finely pitted; the terminal walls straight or curved and finely pitted. Cells (2), the upper and lower and terminal walls thin, very finely and obscurely pitted; the pits on the lateral walls forming a coarse, sieve-plate structure.

Tangential.— Rays medium to high, numerous, 1-seriate, very sparingly resinous, sometimes 2-seriate. The cells (1) somewhat variable, oblong and narrow or broader and oval, unequal. Cells (2) not conspicuously different but the terminal ones sometimes higher, the interspersed ones sometimes narrow.

2. *P. monilifera* Ait.

Transverse.— Growth rings medium to narrow, the limiting wood parenchyma devoid of resin, in 2 to 3 rows. Vessels numerous throughout, broadly oval, becoming rather abruptly fewer at the outer limits of the ring, chiefly single, or less frequently 2- to 3-compounded. Medullary rays prominent, numerous, very sparingly resinous, and distant upwards of 6 rows of wood cells, one cell wide.

Radial.— Rays sparingly resinous, the cells contracted at the ends. Cells (1), the upper and lower walls rather thick, unequal, and finely pitted; the terminal walls thick, straight or curved, and finely pitted. Cells (2), the upper and lower walls thick and finely though remotely pitted; the terminal walls often strongly curved, thick, and finely pitted; the pits on the lateral walls round, oval, or sparingly angled, in radial series.

Tangential.— Medullary rays very numerous, low to high, very sparingly resinous, 1-seriate or sometimes 2-seriate in part. Cells (1), uniform in the same ray and oblong, equal but in different rays ranging from very narrowly oblong to rather broadly oblong. Cells (2) not distinguishable.

3. *P. alba* (Linn.).

Transverse. — Growth rings narrow, uniform, the limiting wood parenchyma very sparingly if at all resinous, in 1, sometimes 2 rows. Medullary rays prominent, somewhat resinous, 1 cell wide, distant upwards of 8 or sometimes 10 rows of cells. Vessels broad, oval, or transversely oval, at first predominant, gradually diminishing in size and number outwardly; 1- to 2-, or more rarely 4-compounded.

Radial. — Medullary rays very sparingly resinous. Cells (1), the upper and lower walls rather thick, finely but strongly pitted; the terminal walls straight, often diagonal, finely pitted; equal to about 6 wood cells. straight. Cells (2), the upper and lower walls somewhat thinner and not obviously pitted; the terminal walls conspicuously though finely pitted; the pits on the lateral walls hexagonal, forming a coarse, sieve-plate structure; somewhat variable in height and sometimes rather short.

Tangential. — Rays numerous, very sparingly resinous, medium, 1-seriate. Cells (1) chiefly uniform, narrow, oblong, and equal, but occasionally rays with broader, oval, and somewhat variable and unequal cells. Cells (2), uniform, narrow, somewhat variable, the terminal ones often much higher.

4. *P. tremuloides* Michx.

Transverse. — Growth rings broad, uniform; the limiting wood parenchyma sparingly resinous, in 1 to 2 rows. Vessels at first medium, becoming larger and finally smaller toward the outer limits of the growth ring, broadly oval, 1- to 4- or more rarely 7-compounded. Medullary rays rather numerous, one cell wide, sparingly resinous, distant upwards of 10 rows of wood cells.

Radial. — Ray cells sparingly resinous, straight. Cells (1), the upper and lower walls thin, and finely pitted; the terminal walls thin, straight or curved, and rarely pitted. Cells (2), the upper and lower walls thin and sparingly pitted; the terminal walls rarely pitted, often curved; the pits on the lateral walls round, chiefly in radial series.

Tangential.— Rays numerous, resinous, low to high, 1-seriate. The cells (1), uniform, narrowly oblong and equal, low rays sometimes showing broader and oval cells throughout. Cells (2) not readily distinguishable, but in low rays sometimes twice as high and less resinous.

5. *P. pyramidalis* Ait.

Transverse. — Growth rings rather broad, uniform; the limiting wood parenchyma in 1 to 2 rows, sparingly resinous. Vessels very numerous, broad, becoming gradually smaller toward the outer limits of the growth ring; 1- to 3-, more rarely 4-compounded. Medullary rays prominent, narrow, one cell wide, numerous, and distant upwards of 7, more rarely 10 rows of cells; somewhat resinous.

Radial. — Medullary rays sparingly resinous; the cells straight, becoming much shorter in the region of the summer wood. Cells (1), the upper and lower walls thin and strongly pitted throughout; the terminal walls finely pitted. Cells (2), the upper and lower walls thin and sparingly pitted; the terminal walls finely pitted; the pits on the lateral walls round or sparingly angled.

Tangential. — Rays very numerous, resinous, medium to high, narrow, 1-seriate. The cells (1) chiefly uniform, rather narrowly oblong and equal in the same ray, but in different rays sometimes varying to broadly oblong. Cells (2) not readily distinguishable except by their less resinous contents and somewhat more variable form and unequal size, usually giving the ray a diminishing terminal width.

6. *P. grandidentata* Michx.

Transverse. — Growth rings narrow, uniform; the limiting wood parenchyma with thin-walled cells in 1 to 3 rows, often very resinous. Vessels numerous throughout the growth ring but usually much smaller near the outer limits of the ring; 1- to 4-, more rarely 5-compounded. Medullary rays prominent but narrow, 1 cell wide and distant upwards of 10 or sometimes 12 rows of cells; somewhat resinous.

Radial. — Ray cells straight. Cells (1), the upper and lower walls thin and entire or obscurely pitted; the terminal walls thin, straight, or curved, finely pitted. Cells (2), the upper and lower walls rather thin and not obviously pitted; the terminal walls often strongly curved, rather thick, and conspicuously pitted; the pits on the lateral walls oval or round in radial series. Isodiametric, thin-walled idioblasts, containing each a single crystal of calcium oxalate of the quadratic system, often form extensive, longitudinal series adjacent to vessels.

Tangential. — Medullary rays numerous, narrow and high, strictly 1-seriate, resinous. The cells (1) chiefly uniform in the same ray and narrowly oblong, equal; but between different rays varying to oblong. Cells (2) not very readily distinguishable, but usually less resinous and often variable from narrowly oblong to oval so as to give the same ray a conspicuously unequal width.

7. *P. wislizeni* Watson.

Transverse. — Growth rings broad; the limiting wood parenchyma sparingly resinous in 1 to 3 rows. Vessels at first predominant, gradually diminishing in size and number toward the outer limits of the growth ring; 1- to 3-, more rarely 4- to 5-compounded. Medullary rays prominent, narrow, one cell wide, distant upwards of 10 rows of cells, numerous, sparingly resinous.

Radial. — Ray cells straight, equal to about 14 wood cells but becoming very short toward the outer limits of the growth ring. Cells (1), the upper and lower and terminal walls rather thin, rather obscurely and finely pitted; the pits on all the walls becoming much more prominent in the outer region of the growth ring. Cells (2), the upper, lower, and terminal walls not very different from (1); the pits on the lateral walls forming a coarse sieve-plate structure.

Tangential. — Rays numerous, narrow, medium to high, sparingly resinous, 1-seriate. Cells (1) uniform, narrowly oblong, and equal, sometimes becoming broader and oval in the central tract so as to form tapering extremities to the ray. Cells (2) not readily distinguishable but uniform, narrow, oblong, and equal.

8. *P. balsamifera* Linn.

Transverse. — Growth rings medium, uniform; the limiting wood parenchyma conspicuously resinous, of one or sometimes two rows of cells. Vessels numerous, oval, becoming gradually smaller toward the outer limits of the growth ring; 1- to 4- or more rarely 5-compounded. Medullary rays numerous, prominent, resinous, one cell wide, and distant upwards of 8 rows of cells.

Radial. — Rays strongly resinous, the cells straight. Cells (1), the upper and lower walls thin and finely pitted; the terminal walls straight or curved, obscurely if at all pitted. Cells (2), the upper, lower, and terminal walls thin and obscurely if at all pitted; the pits on the lateral walls round, in radial series.

Tangential. — Rays very numerous, strongly resinous, low to high, 1-seriate. Cells (1) uniform in the same ray and oblong, but varying between different rays from narrowly oblong to broadly oblong, equal. Cells (2) not distinguishable except by their less resinous contents.

9. *P. angustifolia* James.

Transverse.— Growth rings broad; the limiting wood parenchyma conspicuously resinous, usually upwards of 3 rows of cells thick. Vessels at first somewhat predominant, gradually diminishing in number and finally in size toward the outer limits of the growth ring where they are very much reduced in size; 1- to 4-, rarely 6-compounded. Medullary rays numerous, prominent, resinous, 1 cell wide, distant upwards of 9 rows of cells.

Radial.— Ray cells straight. Cells (1), the upper and lower walls unequally rather thick and strongly pitted; the terminal walls rather thick and strongly pitted. Cells (2), the upper and lower walls sparingly pitted; the terminal walls thin and sparingly if at all pitted; the pits on the lateral walls round or oval and radially seriate.

Tangential.— Medullary rays numerous and very variable, low to high, narrow, resinous, 1-seriate. Cells (1) uniform in the same ray and chiefly very narrowly oblong, equal, but in some rays becoming twice as broad and oblong. Cells (2) not distinguishable.

10. *P. trichocarpa* Torr. & Gr.

Transverse.— Growth rings very broad; the limiting wood parenchyma sparingly resinous. Vessels numerous throughout, becoming abruptly smaller in the outer limits of the growth ring; 1- to 4-compounded. Medullary rays narrow but rather prominent and somewhat resinous; one cell wide, numerous and distant upwards of 12 rows of cells.

Radial.— Ray cells straight. Cells (1), the upper and lower walls thin and not obviously pitted except in the outer limits of the growth ring; the terminal walls straight or curved, and finely pitted. Cells (2), the upper and lower walls usually thick and more or less strongly pitted; the terminal walls rather thick and strongly pitted; the lateral walls with round or sparingly angled and radially seriate pits.

Tangential.— Rays rather numerous, resinous, high, narrow, strictly 1-seriate. Cells (1) chiefly uniform, narrowly oblong and equal, in a few rays becoming broader and oblong, somewhat unequal. Cells (2) not readily distinguishable.

11. *P. heterophylla* Linn.

Transverse.— Growth rings medium, rather uniform; the limiting wood parenchyma not very prominent, usually one cell thick and often forming a discontinuous zone. Vessels numerous and large, oval or round, often in series continuous and compounded with those of the previous year, diminishing steadily in size toward the outer face of the growth ring; chiefly single but often 2-, or on the outer face of the growth ring sometimes 3-compounded. Medullary rays not very prominent, 1 cell wide, rather numerous and distant upwards of 6 or more rarely 10 rows of cells.

Radial.— Medullary rays non-resinous. Cells (1), the upper and lower walls, as also the terminal walls, usually rather thick and strongly pitted. Cells (2), the upper and lower walls somewhat thinner, less strongly pitted; the terminal walls strongly pitted; the lateral walls with round, oval, or sparingly angled pits.

Tangential.— Medullary rays numerous, rather high, non-resinous, narrow, 1 cell wide. Cells (1) chiefly uniform in the same ray, oblong and equal, but between different rays varying from narrowly oblong to rather broadly oblong. Cells (2) not distinguishable from the first.

2. Salix.

Radial.— Ray cells (1) usually low and thick-walled, several times longer than high; the upper and lower and terminal walls commonly pitted. Cells (2) often thin-walled, marginal, and interspersed, commonly predominant, very variable, short, and often several times higher than long; the pits on the lateral walls more definitely angled, forming more extensive and finer sieve-plates, and sometimes merging into definite scalariform structure.

Tangential.— Ray cells clearly distinguishable as of two kinds.

SYNOPSIS OF SPECIES.

Pits on the lateral walls of the ray cells (2) angled or oval and merging into an open, scalariform structure.

  Resinous wood parenchyma prominent throughout in association with the vessels.

    Rays (tangential) narrow, the cells (1) uniform, narrow and oblong.

      Vessels oval, 1- to 2- or more rarely 3-compounded. . 13. *S. sessilifolia.*

  Resinous wood parenchyma confined to the outer limits of the growth ring.

    Rays (tangential) numerous, resinous, and chiefly narrow. Cells (1) somewhat variable, chiefly oblong and narrow, more rarely oval, more or less conspicuously unequal.

      Vessels broad (transverse), oval, 1- to 4- or finally 4- to 5-compounded. . . . . . . 14. *S. amygdaloides.*

    Rays (tangential) resinous, numerous, broader; cells (1) variable, oblong to broadly oval and conspicuously unequal.

      Vessels (transverse) predominant throughout, oval, 2- to 4- or finally 5-compounded. . . . . . . 15. *S. discolor.*

    Rays (tangential) broad, more or less 2-seriate; the cells (1) variable, oval to oblong and conspicuously unequal.

      Vessels (transverse) chiefly single throughout, but sparingly 2- to 3-compounded. . . . . . . 12. *S. lasiolepis.*

Pits on the lateral walls of the ray cells (2) hexagonal or quadrangular, forming coarse sieve-plates, but devoid of scalariform structure.

  Resinous wood parenchyma conspicuous throughout the growth ring.

    Resinous wood parenchyma confined to the vessels and the limiting zone.

      Rays (tangential) numerous, resinous, 2-seriate in part; the cells (1) variable, narrowly to broadly oval, or round, or even squarish, very unequal. . . . . . 10. *S. longifolia.*

    Resinous wood parenchyma numerous and often forming definite tracts.

      Rays (tangential) very numerous, narrow; cells (1) uniform, oval, and chiefly equal throughout. . . . . . 11. *S. cordata.*

  Resinous wood parenchyma confined to the limiting zone.

    Rays (tangential) narrow, 1-seriate.

      Ray cells (1) variable, oblong, narrow or more often broadly oval or squarish, unequal.

        Vessels (transverse) at first broadly oval; 1- to 3- or finally 8-compounded and narrow. . . . . . 4. *S. nigra.*

      Ray cells (1) uniform in the same ray but variable between different rays, narrowly oblong to oblong, chiefly equal.

Vessels (transverse) strongly predominant throughout, 2- to 3- or more rarely 4-compounded. . . . . 5. *S. alba.*

Ray cells (1) somewhat variable, chiefly oblong or sometimes broadly oval; chiefly equal.

Vessels (transverse) strongly predominant, 2- to 5-compounded. 6. *S. lasiandra.*

Ray cells (1) chiefly uniform and oblong, sometimes oval; unequal, often twice as broad or twice as high.

Vessels (transverse) large, strongly predominant, 2- to 3- or rarely 4-compounded. . . . . . . 7. *S. lancifolia.*

Ray cells (1) uniform, oblong, chiefly equal.

Vessels (transverse) predominant, at first large, chiefly simple but 2- or very sparingly 3-compounded. 8. *S. brachystachys.*

Ray cells (1) narrow, chiefly uniform, oval or more generally oblong, equal.

Vessels (transverse) uniform in size and number throughout, except at the outer limits of the growth ring where they abruptly diminish in size; chiefly 1- often 2- to 3-compounded. . . . . 9. *S. scouleriana.*

Rays (tangential) broader, more or less 2-seriate.

Ray cells (1) uniform in the same ray, variable between different rays, oval or squarish, broad, unequal.

Vessels (transverse) predominant, 2- to 3- or more rarely 5-compounded. . . . . 1. *S. lævigata.*

Ray cells (1) uniform, oval, narrow, chiefly equal.

Vessels (transverse) single or somewhat 2- to 3-compounded. 2. *S. hookeriana.*

Ray cells (1) thin-walled, uniform, oblong, narrowly oval, equal.

Vessels (transverse) not predominant, 1- to 4-compounded, conspicuously fewer toward the outer limits of the growth ring. 3. *S. uva-ursi.*

1. *S. lævigata* Bebb.

Transverse.—Growth rings very broad; the limiting wood parenchyma about 3 cells thick, sparingly resinous. Vessels predominant throughout, at first rather large, radially oblong and very gradually reduced in size to the outer limits of the growth ring where they are about $\frac{1}{4}$ the original dimensions; 2- to 3- more rarely 5-radially compounded. Medullary rays numerous, resinous, prominent, 1 cell wide, distant upwards of 6 rows of cells.

Radial.— Rays resinous. Cells (1), the upper and lower walls thin and not pitted; the terminal walls finely pitted. Cells (2) sometimes predominant; the upper and lower walls thin and not pitted; the terminal walls finely pitted; the pits on the lateral walls forming a coarse sieve-plate structure.

Tangential.— Rays very numerous, medium to rather broad, 2-seriate in part, resinous. Cells (1) uniform in the same ray but variable in different rays, oval or squarish, unequal. Cells (2) uniform and narrowly oblong, strongly unequal, often several times higher than broad.

2. *S. hookeriana* Burr.

Transverse.— Growth rings very broad; the limiting wood parenchyma composed of rather distant and resinous cells. Vessels rather numerous, single or somewhat 2- to 3-compounded, oval, very gradually diminishing in size to the outer limits of the growth ring where they are $\frac{1}{4}$ to $\frac{1}{3}$ the diameter of the first. Medullary rays numerous, slightly resinous, 1 cell wide, distant upwards of 8 rows of cells.

Radial.— Rays rather sparingly resinous. Cells (1) more resinous; the upper and lower walls thick and very unequally, often sparingly pitted; the terminal walls rather strongly though finely pitted. Cells (2) less resinous, the upper and lower walls rather thin and devoid of pits; the terminal walls strongly and finely pitted; the pits on the lateral walls minute, simple and often slit-like when opposite wood cells, but forming a coarse sieve-plate structure opposite vessels.

Tangential.— Rays numerous, resinous, sometimes 2-seriate in part, low to high, narrow. Cells (1) rather uniform and oval, chiefly equal. Cells (2) variable, narrowly oblong and more or less conspicuously unequal, rather thin-walled.

3. *S. uva-ursi* Pursh.

Transverse. — Growth rings narrow, variable, eccentric; the limiting wood parenchyma rather resinous and prominent; the wood cells thin-walled and squarish throughout with no obvious distinction of spring and summer wood. Vessels not predominant, 1- to 4-compounded and conspicuously few toward the outer face of the growth ring. Medullary rays 1 cell wide, very sparingly resinous, not prominent, distant upwards of 6 rows of wood cells.

Radial. — Medullary rays sparingly resinous. Cells (1), the upper and lower walls usually thin and not obviously pitted; the terminal walls somewhat strongly pitted. Cells (2), the upper and lower walls thin and not obviously pitted; the terminal walls finely pitted; the pits on the lateral walls forming a strong sieve-plate structure; strongly predominant.

Tangential. — Medullary rays low to medium, very narrow, sparingly resinous, 2-seriate in part, the cells chiefly thin-walled throughout. Cells (1) uniform, oblong, to narrowly oval; equal. Cells (2) uniform, narrowly oblong, unequal, and often several times higher than broad; usually predominant and often excluding (1).

4. *S. nigra* Marsh.

Transverse.— Growth rings broad, the inner region of the growth ring usually more dense; the limiting wood parenchyma sparingly resinous, in 1 to 2 rows of cells. Vessels numerous, large, rather broad, and oval, gradually diminishing in size and number toward the outer region of the growth ring and finally becoming few, narrow, and rather small; 1- to 3-compounded or in the outer portions of the ring often 8-compounded and narrow. Rays rather numerous, not very prominent, very sparingly resinous, 1 cell wide, and distant upwards of 8 rows of wood cells.

Radial.— Medullary rays locally resinous. Cells (1), the upper and lower walls rather thin and usually not obviously pitted; the terminal walls chiefly thin and devoid of pits. Cells (2), the upper and lower walls thin and devoid of pits; the terminal walls strongly but finely pitted; the pits on the lateral walls forming a strong sieve-plate structure.

Tangential.— Rays very numerous, medium, sparingly resinous, 1-seriate, and broad. Cells (1), variable, unequal, oblong and narrow or more often broad and oval or squarish; unequal. Cells (2) less resinous, variable but chiefly narrowly oblong, unequal, and differing in both height and width.

5. *S. alba* Linn.

Transverse.— Growth rings very broad, the limiting wood parenchyma 1 to 2 cells thick, resinous. Vessels strongly predominant throughout; large, oval, often oblong, chiefly single but often 2- to 3- or more rarely 4-compounded; not diminishing sensibly toward the outer face of the growth ring. Medullary rays numerous, somewhat resinous, 1 cell wide, distant upwards of 8 rows of wood cells.

Radial.— Rays sparingly resinous. Cells (1), the upper and lower walls thick, and strongly pitted throughout, the terminal walls generally curved and strongly pitted. Cells (2), the upper and lower and terminal walls strongly pitted; the pits on the lateral walls forming a strong sieve-plate structure; often approximating in height and general character to cells (1).

Tangential.— Rays resinous, numerous, narrow, medium. Cells (1) uniform in the same ray but variable in different rays, and ranging from narrowly oblong to oblong; chiefly equal. Cells (2) less resinous, uniform but unequal, differing greatly in height.

6. *S. lasiandra* Benth.

Transverse.— Growth rings broad; the limiting zone of wood parenchyma continuous, conspicuous and resinous, 1 to 2 cells thick. Vessels strongly predominant, radially and somewhat tangentially 2- to 5-compounded, steadily diminishing in size to the outer limits of the growth ring where they are reduced to $\frac{1}{2}$ or $\frac{1}{3}$ the first size. Rays somewhat resinous, prominent, 1 cell wide, distant upwards of 6 rows of wood cells.

Radial.— Rays somewhat resinous. Cells (1), the upper and lower walls rather thick and often strongly pitted; the terminal walls thick and strongly though finely pitted. Cells (2) more resinous, often predominant; the upper and lower walls thin and not pitted; the terminal walls thicker and strongly though finely pitted, the pits on the lateral walls forming a prominent sieve-plate structure.

Tangential. — Rays numerous, resinous, narrow, chiefly medium. Cells (1) somewhat variable, chiefly oblong or again broadly oval; chiefly equal. Cells (2) uniform and narrowly oblong; very unequal and often several times higher than broad.

7. *S. lancifolia* Anderss.

Transverse.— Growth rings broad; the limiting wood parenchyma resinous and prominent. Vessels rather large and strongly predominant throughout, radially oval and 2- to 3- rarely 4-compounded; diminishing very gradually in size to the outer limits of the growth ring where they are about two thirds the first diameter. Medullary rays numerous, resinous, and prominent, 1 cell wide, distant upwards of 6 rows of cells.

Radial.— Rays resinous. Cells (1), the upper and lower walls thick and unequally though often strongly pitted; the terminal walls thick and strongly though finely pitted. Cells (2), the upper and lower and terminal walls thick and strongly pitted; the pits on the lateral walls forming a coarse sieve-plate structure.

Tangential.— Rays numerous, resinous, narrow, medium. Cells (1) chiefly uniform and oblong, but varying somewhat from oval to oblong; unequal and often twice as broad or twice as high. Cells (2) much less resinous, uniform, narrowly oblong, unequal.

8. *S. brachystachys* Benth.

Transverse.— Growth rings broad; the limiting zone of wood parenchyma not resinous. The wood cells large, rather thin-walled throughout. Vessels predominant throughout; at first large, radially oval, chiefly single but 2- or very sparingly 3-compounded; gradually diminishing in size to the outer limits of the growth ring where they become 2- to 5-compounded. Medullary rays numerous, non-resinous, 1 cell wide, distant upwards of 10 rows of cells.

Radial.— Rays non-resinous. Cells (1), the upper and lower walls rather thin and not obviously pitted; the terminal walls with very fine pits. Cells (2), the upper and lower walls thin and not pitted; the terminal walls somewhat thicker and very finely pitted; the pits on the lateral walls forming a coarse, sieve-plate structure.

Tangential.— Rays numerous, narrow, low to rather high, somewhat resinous. Cells (1) uniform, oblong, chiefly equal. Cells (2) uniform, narrowly oblong, very unequal, and often several times higher than broad.

Transverse.— Growth rings medium; the limiting zone of wood parenchyma somewhat resinous, 1 to 3 cells thick. Vessels somewhat uniform in size and number throughout, except at the outer limits of the growth ring where they abruptly diminish in size; oval, rather broad, chiefly 1-, but frequently 2- to 3- more rarely 4-compounded. Medullary rays numerous, prominent, resinous, 1 cell wide, and distant upwards of 8 rows of cells.

Radial.— Medullary rays resinous. Cells (1), the upper and lower and terminal walls thick and strongly pitted throughout. Cells (2), the upper and lower and terminal walls rather thick and strongly pitted; the pits on the lateral walls forming a prominent sieve-plate structure.

Tangential.— Rays numerous, resinous, medium, narrow, 1-seriate. Cells (1) narrow, chiefly uniform, oval or more generally oblong, equal. Cells (2) uniform, narrowly oblong but very unequal, and often several times higher.

10. *S. longifolia* Muhl.

Transverse.— Growth rings usually very broad but very variable and sometimes very narrow. Wood parenchyma cells numerous, very resinous, and associated with the vessels as well as forming an open zone on the outer face of the growth ring. Vessels predominant throughout, especially in the earlier portions of the growth ring; at first rather large, oval, and 1- to 3-compounded, later somewhat reduced, round, and simple or somewhat 2-compounded. Medullary rays numerous, resinous, 1 to 2 cells wide, distant upwards of 6, or more rarely 10 rows of wood cells.

Radial.— Medullary rays resinous. Cells (1), the upper and lower walls sparingly pitted, the terminal walls strongly but finely pitted. Cells (2), the upper and lower walls rather thick but not obviously pitted, the terminal walls very strongly pitted; the pits on the lateral walls forming a coarse sieve-plate structure.

Tangential.— Rays very numerous, resinous, 2-seriate in part. Cells (1) very variable, from narrowly to broadly oval, or round, or even squarish, very unequal. Cells (2) uniform, narrowly oblong but unequal and generally with thinner walls.

11. *S. cordata* Muhl.

Transverse.— Growth rings broad, terminated by 2 to 3 rows of radially flattened, rectangular wood cells; the limiting wood parenchyma prominent, resinous ; the structure rather dense throughout. Vessels not predominant ; at first very numerous and very resinous, quickly diminishing in number and thence constantly diminishing in size and number, and always distant, to the outer face of the growth ring ; rather small, oval, sparingly 2- or more rarely upwards of 4-compounded ; everywhere numerous. Resinous wood parenchyma cells numerous throughout ; associated with vessels and scattering throughout the growth ring, often forming more or less definite and extensive tracts. Medullary rays very numerous, resinous, 1 cell wide, distant upwards of 10 rows of cells.

Radial.— Ray cells very resinous. Cells (1), the terminal walls very thick and very strongly pitted ; the upper and lower walls sparingly if at all pitted except in the later portions of the growth ring. Cells (2), often predominant ; the upper and lower walls thin and not pitted except in the later portions of the growth ring ; the terminal walls strongly pitted ; the pits on the lateral walls forming a coarse sieve-plate structure.

Tangential.— Rays very numerous, medium, narrow, resinous. Cells (1) uniform, oval, and chiefly equal throughout. Cells (2) variable, oblong, often very narrow and unequal, often several times higher than broad, the walls commonly thinner.

12. *S. lasiolepis* Torr.

Transverse.— Growth rings broad ; the limiting wood parenchyma 1 to 4 cells thick, sparingly resinous. Vessels at first not strongly predominant ; oval or oblong, steadily diminishing in size and finally much reduced ; chiefly single throughout, but sparingly 2- to 3-compounded. Medullary rays numerous, locally resinous, 1 to 2 cells wide, distant upwards of 6 rows of wood cells.

Radial. — Medullary rays resinous. Cells (1), the upper and lower walls sparingly and unequally pitted, often devoid of pits ; the terminal walls strongly but finely pitted. Cells (2), the upper and lower walls chiefly rather thin and devoid of pits ; the terminal walls strongly pitted ; the pits on the lateral walls forming a coarse sieve-plate structure often coalescing into a coarse scalariform structure.

Tangential. — Rays very numerous, medium, resinous, 1- to 2-seriate. Cells (1) variable, oval to oblong, and conspicuously unequal. Cells (2) less resinous, variable, and unequal, often high.

13. *S. sessilifolia* Nutt.

Transverse.— Growth rings broad ; the limiting wood parenchyma 1 to 2 rows of cells broad, occasionally resinous and confluent with resinous wood parenchyma in the adjacent spring wood. Vessels numerous and predominant throughout ; radially oval and variable in size ; 1- to 2-, more rarely 3-compounded, especially at the outer limits of the growth ring where they are diminished to $\frac{1}{4}$ size. Resinous wood parenchyma more or less prominent throughout the growth ring in association with the vessels. Medullary rays numerous, rather prominent and resinous, 1 cell wide, distant upwards of 10 rows of wood cells.

Radial.— Rays somewhat resinous. Cells (1), the upper and lower and terminal walls strongly though rather finely pitted throughout, more resinous than the next. Cells (2) less resinous, often predominant; the upper and lower walls rather thin and sparingly pitted; the terminal walls strongly though finely pitted; the pits on the lateral walls variable, hexagonal, and forming a coarse; sieve-plate structure which more commonly becomes an open scalariform structure through transitional forms.

Tangential.— Rays sparingly resinous, low to medium, numerous, narrow. Cells (1) chiefly uniform, narrow, oblong, equal. Cells (2) uniform, narrowly oblong, very unequal and often several times higher than broad, less resinous than (1).

14. *S. amygdaloides* Anderss.

Transverse.— Growth rings broad; the limiting zone of wood parenchyma 1 to 4 cells thick and not obviously resinous. Vessels broad, oval, at first predominant, soon diminishing slightly in size and number toward the outer face of the growth ring where they are again somewhat abruptly reduced in size; at first oval, rather broad, and 1- to 4-compounded; finally much reduced in size and width and becoming 4- to 5-compounded. Medullary rays numerous, 1 cell wide, not resinous, and distant upwards of 16 rows of wood cells.

Radial.— Medullary rays more or less resinous. Cells (1), the upper, lower, and terminal walls rather thin and finely, the first obscurely if at all pitted. Cells (2), the upper and lower and terminal walls rather thin, the last finely but conspicuously pitted; the pits on the lateral walls forming a coarse sieve-plate structure often coalescing to form an open scalariform structure.

Tangential.— Rays very numerous, resinous, medium, chiefly narrow, 1-seriate. Cells (1) somewhat variable, oval or chiefly oblong and narrow, more or less conspicuously unequal. Cells (2) chiefly uniform, unequal, often several times higher.

15. *S. discolor* Muhl.

Transverse.— Growth rings broad, the limiting zone of wood parenchyma chiefly resinous. Vessels predominant throughout, radially oval, and 2- to 4-, more rarely 5-compounded especially at the outer limits of the growth ring, where they are diminished to $\frac{1}{2}$ size. Medullary rays resinous, prominent and numerous, 1 cell wide; distant upwards of 6 rows of wood cells.

Radial.— Rays resinous. Cells (1), the upper and lower and terminal walls thick, strongly but finely pitted. Cells (2), the upper and lower and terminal walls thick, finely but strongly pitted; marginal and interspersed, often predominant; the pits on the lateral walls variable and hexagonal, and forming a coarse sieve-plate structure which often passes through transitional forms into a scalariform structure.

Tangential.— Medullary rays resinous, numerous, low to high. Cells (1) variable, oblong to broadly oval, and conspicuously unequal. Cells (2) chiefly uniform and narrow, but very unequal and often several times higher than long, terminal, and interspersed, often predominant.

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ERRATA.

Page 515, line 29, for "Proteaceæ which is preëminently," read Proteaceæ which thus appears to be. Line 30, for "19 : 0.00," read *1 : 0.41*.

Page 516, line 9, for "forty-seven" read *fifty*-seven.

Page 516, first line of table, Proteaceæ, for "19:0.00" read *1:0.41*; for "19" read *24*; for "0.00" read *10* and insert "the whole" in the nineteenth line after Araliaceæ.